

New family-level characters for Platygastroidea

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Abstract

Platygastridae (Hymenoptera) is a diverse family of parasitoid wasps for which few studies of internal morphology have been conducted. The monophyly of the group is undisputed based on recently published molecular data, but based on morphology, the family is diagnosable from other platygastroids only by a combination of character reductions. In the present study we explored the mesosoma of Platygastroidea and found two new synapomorphies for Platygastridae: an externally visible anterior mesofurcal pit, which corresponds to an invagination that connects to the anterior portion of the mesofurca, and internally, a posteriorly shifted origin of the first wing flexors. The absence of a mesofurcal bridge and the exclusively mesopectal origin of the fore wing flexors are treated as synapomorphies for Platygastridae+Janzenellidae. Phylogenetic implications and evolutionary hypotheses regarding these traits are discussed.

Keywords

Fossils, furca, Janzenellidae, morphology, Platygastridae, Scelionidae

Introduction

Platygastridea (Hymenoptera, Proctotrupomorpha) are parasitoid wasps whose hosts represent ten insect orders and spiders (Austin et al 2005; Chen et al. 2021) and has been recently classified into eight families (Table 3; Chen et al. 2021). Platygastridae is highly diverse and extremely common with more than 2000 species worldwide (mbd-db.osu.edu). Based on molecular analyses, Platygastridae is sister to Janzenellidae, but

this relationship is yet to be supported by any morphological characters. Platygasteridae currently contains two monophyletic subfamilies, Platygasterinae and Sceliotrachelinae (Chen et al. 2021).

Platygasterinae parasitize gall midges (Diptera, Cecidomyiidae) (Austin et al. 2005) and are known to be effective against new invasive and serious quarantine pests in North America, such as the Swede midge (Ferland 2020) and the apple leaf midge (He and Wang 2015; Cossentine et al. 2021). They are considered propitious natural enemies of the wheat midge (Echegaray et al. 2016; Chavalle et al. 2018; Dufton et al. 2021) and have potential utility in suppressing populations of the soybean midge as well (Harris 2019; Kee 2019). In contrast to Platygasterinae, sceliotrachelines are egg, nymphal, and larval parasitoids of multiple orders including Coleoptera, Hemiptera, and Hymenoptera (Chen et al. 2021).

Despite their economic importance, the systematics of Platygasteridae at the species level is in major need of revision, characterized by a high number of superficially described species with incomplete or missing differential diagnoses (Buhl and Jałoszyński 2019; Buhl 2021). At the generic level, identification of platygasterines is nearly impossible for non-specialists due to a lack of comprehensive identification keys and inadequate generic concepts.

The monophyly of Platygasteridae is strongly supported by a recent molecular analysis (Chen et al. 2021). Despite this strong support of monophyly, only three morphological synapomorphies have been proposed for the family: absence of a mesepimeral sulcus (Talamas et al. 2019), absence of the mesofurcal bridge (Heraty et al. 1994), and the absence of a netrion (Mikó et al. 2007). However, only the mesepimeral sulcus has been examined in a wide range of platygasterid taxa and on many specimens. In this study, we examined the skeletomuscular system of the mesosoma in a range of extant and fossil platygasteroids to better characterize these and other traits, and to explore to what degree they are phylogenetically informative.

Material and methods

Microscopy

Brightfield images were captured with three different imaging systems: a Z16 Leica lens with a JVC KY-F75U digital camera using Cartograph and Automontage software; an Olympus BX51 compound microscope with a Canon EOS 70D digital SLR camera; and a Leica DM2500 compound microscope with a Leica DFC425 camera. Illumination was achieved with a lighting dome or with LED gooseneck lamps and mylar light dispersers. Images were rendered from Z-stacks with Automontage, Helicon Focus, or Zerene Stacker.

Dissections for scanning electron microscopy were performed with a minuten probe and forceps and body parts were mounted to a 12 mm slotted aluminum mounting stub using a carbon adhesive tab and sputter coated with approximately 70 nm of

gold/palladium using Cressington 108 and Denton IV sputter coaters. Micrographs were captured using Hitachi TM3000 Tabletop and Phenom XL G2 Desktop scanning electron microscopes (SEM)

Specimens were analyzed between two #1.5 coverslips with a Nikon A1R-HD Confocal Laser Scanning Microscope (CLSM) at the University of New Hampshire Instrumentation Center using three excitation wavelengths (409, 487, and 560 nm), and three emission ranges of (435–470, 500–540, and 570–645 nm). Pseudo-colors of CLSM micrographs reflect their fluorescence spectra. Media files and volume-rendered micrographs were generated using FIJI (Schindelin et al. 2012).

Material examined

Specimens of the present study (Table 1) were identified using Masner and Huggert (1989), Masner (1980), and Masner (1976). Table 1 contains a list of taxa for which images are available in the figures or can be accessed via the CUID at mbd-db.osu.edu.

Terminology

Morphological terminology follows Mikó et al. (2007), Talamas et al. (2019), and Vilhelmsen et al. (2010) and is aligned to the Hymenoptera Anatomy Ontology (Table 2).

Results

In this section, we provide annotated descriptions of morphological traits on the pronotum and mesopectus that have significance in the higher classification of Platygastroidea with special emphasis on Platygastriidae. Numbers following each trait description represent characters: states indicated in Table 3.

Description

The netrion is absent (1:0; Figs 1–4) from Platygastriidae and Janzenellidae, and the first flexor of the fore wing arises exclusively from the mesopectus (2:0; Fig. 23B, C). The netrion is present (1:1) in Nixoniidae, Scelionidae, and Sparasionidae, and the first flexor of the fore wing arises partially from the pronotum (site of origin of the muscle corresponds to netrion, 2:1; Fig. 23A). The muscle was not observed in other platygastroid families that we examined. The ventral bridge of the pronotum is visible laterally, directly anterior to the ventral mesopectus (3:1; Fig. 4) in some platygastroid genera (*Allostemma*, *Alfredella* Masner & Huggert, *Amitus*, *Oligomerella* Masner & Huggert, *Prototeleia* Talamas, Popovici, Shih & Ren), but the first flexor of the fore wing does not partially originate from that area. The ventral bridge of the pronotum is visible laterally in some Proterosceliopsidae but not in other families of Platygastroidea.

Table 1. Imaging techniques, localities, depositories and family classification for the specimens examined.

Collection	Collecting Unit Identifier (CUID)	Family/ Subfamily	Genus/species	Imaging method	Origin	Figure
UNHC	FSCA 00000289	Platygastrinae	<i>Allostemma</i> sp. Masner & Huggert, 1989	Confocal Laser Scanning LSM	USA	19
USNM	USNMENT01197966	Platygastrinae	<i>Allostemma bicolor</i> Buhl & Choi, 2006	SEM	South Korea	
USNM	USNMENT00872678	Platygastrinae	<i>Euxestonotus</i> sp. Fouts, 1925	SEM	Nicaragua	
USNM	USNMENT01109601_1	Platygastrinae	<i>Inostemma</i> sp. Haliday, 1833	SEM	USA	
USNM	USNMENT01029164	Platygastrinae	<i>Iphitrachelus</i> sp. Halliday, 1835	SEM	Dominica	3
USNM	USNMENT01109601_4	Platygastrinae	<i>Isostasius</i> sp. Förster, 1856	SEM	USA	
OSUC	OSUC 334137	Platygastrinae	<i>Isocybus</i> sp. Förster, 1856	brightfield imaging	USA	16
OSUC	unvouchered	Platygastrinae	<i>Isocybus</i> sp. Förster, 1856	brightfield photography	USA	17
USNM	USNMENT00872560	Platygastrinae	<i>Leptacis</i> sp. Förster, 1856	SEM	Kenya	
USNM	USNMENT01059861	Platygastrinae	<i>Metaclisis</i> sp. Förster, 1856	SEM	USA	
USNM	USNMENT01109899	Platygastrinae	<i>Orseta</i> sp. Masner & Huggert, 1989	compound microscope	Brazil	
USNM	USNMENT00872580	Platygastrinae	<i>Piestopleura</i> sp. Förster, 1856	SEM	Kenya	
USNM	USNMENT00872803	Platygastrinae	<i>Platygaster</i> sp. Latreille, 1809	SEM	USA	
USNM	USNMENT01197981_1	Platygastrinae	<i>Sacespalus</i> sp. Kieffer, 1917	SEM	SE Asia	
USNM	USNMENT00872647	Platygastrinae	<i>Synopeas</i> sp. Förster, 1856	SEM	Kenya	
UNHC	UNHC_1046722A	Platygastrinae	<i>Synopeas</i> sp. Förster, 1856	CLSM	USA	18
UNHC	UNHC_1046722B	Platygastrinae	<i>Synopeas</i> sp. Förster, 1856	compound microscope	USA	5
USNM	USNMENT00989620_2	Platygastrinae	<i>Trichacis</i> sp. Förster, 1856	SEM	USA	
UNHC	FSCA 00000276	Platygastrinae	<i>Trichacis</i> sp. Förster, 1856	CLSM	USA	14
CNCI	OSUC 334109	Platygastrinae	<i>Almargella cristata</i> Masner & Huggert, 1989	brightfield photography	Chile	
CNCI	OSUC 334127	Platygastrinae	<i>Rao</i> sp. Masner & Huggert, 1989	brightfield photography	Australia	
USNM	USNMENT00989622_2	Sceliotrachelinae	<i>Amitus</i> sp. Haldeman, 1850	SEM	USA	1
UCRC	UNHC_1046725A	Sceliotrachelinae	<i>Amitus</i> sp. Haldeman, 1850	CLSM	USA	15
UCRC	UNHC_1046725B	Sceliotrachelinae	<i>Amitus</i> sp. Haldeman, 1850	compound microscope	USA	6
FSCA	OSUC 698061	Sceliotrachelinae		SEM	Madagascar	4
USNM	USNMENT01197842	Sceliotrachelinae	<i>Calomerella scutellata</i> Masner & Huggert, 1989	brightfield photography	USA	
USNM	USNMENT01197841	Sceliotrachelinae	<i>Errolium</i> sp. Masner & Huggert, 1989	brightfield photography	New Zealand	
FSCA	OSUC 698059	Sceliotrachelinae	<i>Fidiobia</i> sp. Ashmead, 1894	SEM	Madagascar	2
CNCI	USNMENT00989211	Sceliotrachelinae	<i>Helava alticola</i> Masner & Huggert, 1989	SEM	Colombia	
FSCA	OSUC 698060	Sceliotrachelinae	<i>Isolia</i> sp. Förster, 1878	SEM	Madagascar	
ANIC	ANIC 32 153903	Sceliotrachelinae	<i>Oligomerella donnae</i> Masner & Huggert, 1989	brightfield photography	Australia	
USNM	USNMENT01059128	Sceliotrachelinae	<i>Parabaeus</i> sp. Kieffer, 1910	SEM	Brazil	
FSCA	OSUC 698062	Sceliotrachelinae	<i>Pulchrisolia teras</i> Lahey, 2019	SEM	Madagascar	
SAMC	SAM-HYM-P084755	Sceliotrachelinae	<i>Sceliotrachelus karoensis</i> van Noort, 2021	SEM	South Africa	
USNM	USNMENT01197878	Sceliotrachelinae	<i>Tetrabaeus</i> sp. Kieffer, 1912	brightfield photography	Canada	
CNU	CNU-HYM-MA-2016107	Sceliotrachelinae		compound microscope	Myanmar	22
USNM	OSUC 226542	Platygastridae	<i>Orwellium enigmaticum</i> Johnson, Masner & Musetti, 2009	SEM	Chile	7
USNM	OSUC 163002	Sparasionidae	<i>Archaeoteleia gracilis</i> Masner, 1968	SEM	Chile	9
CNU	CNU-HYM-MA-2017545	Scelionidae	<i>Proteroscelio</i> sp. Brues, 1937	fluorescence microscope	Myanmar	12
FSCA	DPI_FSCA 00008713	Scelionidae	<i>Gryon aetherium</i> Talamas, 2021	CLSM	USA	13
CNCI	OSUC 148693	Geoscelionidae	<i>Huddlestonium exu</i> Polaszek & Johnson, 2007	brightfield photography	Ivory Coast	

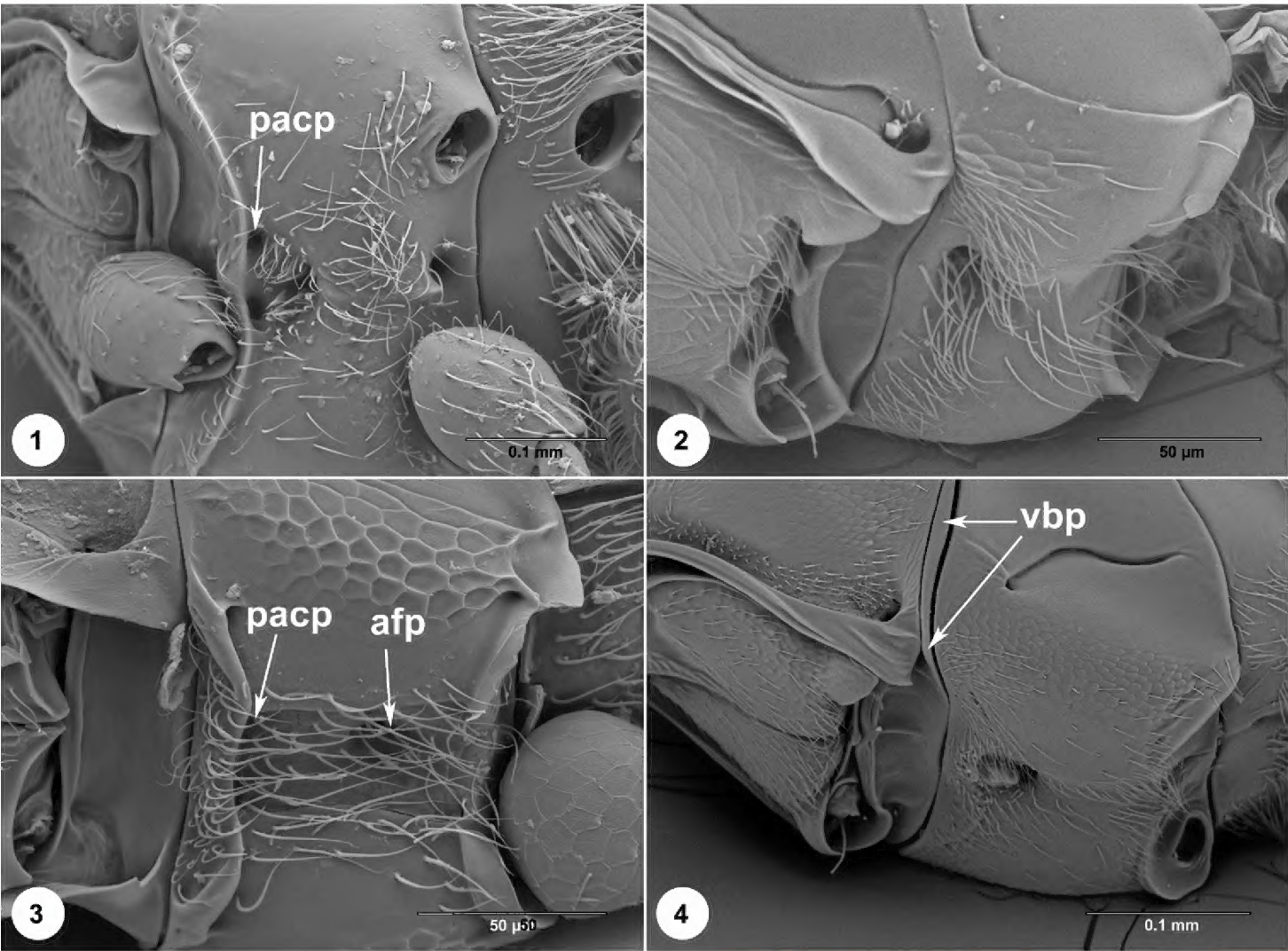
Collection	Collecting Unit Identifier (CUID)	Family/Subfamily	Genus/species	Imaging method	Origin	Figure
USNM	OSUC 264384	Janzenellidae	<i>Janzenella innupta</i> Masner & Johnson, 2007	SEM	Costa Rica	8
UNHC	UNHC_0032469	Janzenellidae	<i>Janzenella innupta</i> Masner & Johnson, 2007	CLSM, compound microscope	Costa Rica	20–21
SAMC	SAM-HYM-P093322	Nixoniidae	<i>Nixonia</i> sp. Masner, 1958	brightfield photography	South Africa	11
USNM	USNMENT01109338	Nixoniidae	<i>Nixonia watshami</i> Johnson & Masner, 2006	SEM	Botswana	
USNM	USNMENT00989930	Sparasionidae	<i>Sceliomorpha</i> sp. Ashmead, 1893	SEM	Costa Rica	10

Table 2. URI Table of morphological terms and annotations in the figures (Seltmann et al. 2012).

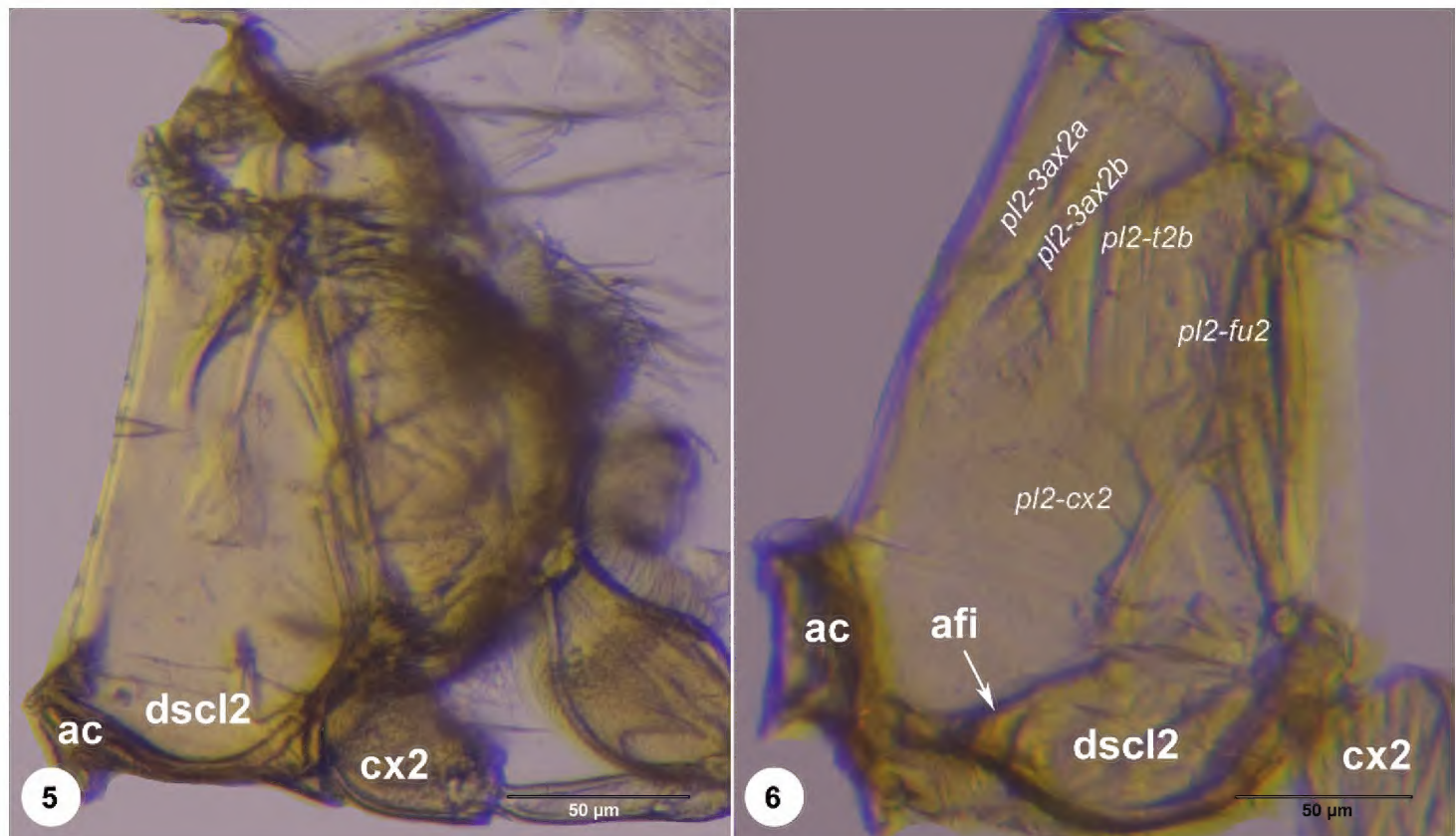
abbreviation	term	HAO definition	Figure references	URI
ac	acetabulum	The scrobe that is located anteroventrally on the mesopectus and accommodates the procoxa.	5–6, 13, 17	http://purl.obolibrary.org/obo/HAO_0000294
afp	anterior mesofurcal pit	The pit that corresponds to the anterior mesofurcal invagination.	3, 7, 14, 16, 22	http://purl.obolibrary.org/obo/HAO_0002559
afi	anterior mesofurcal invagination	The invagination that arises medioventrally from the mespectus, anterior to the mesofurcal pit and is continuous with the invagination of the mesofurca.	6, 15, 17	http://purl.obolibrary.org/obo/HAO_0002560
ats	postacetabular sulcus	The sulcus that extends posteriorly along the acetabular (epicnemial) carina.	9–10	http://purl.obolibrary.org/obo/HAO_0000741
cx1	fore coxa	The coxa that is located on the fore leg.	21–22	http://purl.obolibrary.org/obo/HAO_0001122
cx2	meso coxa	The coxa that is located on the mid leg.	5–6	http://purl.obolibrary.org/obo/HAO_0000635
dscr2	mesodiscrimen	The discrimen that is located in the mesothorax and corresponds with the mesodiscriminal lamella.	8–12	http://purl.obolibrary.org/obo/HAO_0000545
dsc12	mesodiscriminal lamella	The discriminal lamella that is located in the mesothorax.	5–6, 17–18, 20–21, 23A–C	http://purl.obolibrary.org/obo/HAO_0000546
mer	mesepimeral ridge	The ridge that extends along the posterior margin of the mesopectus.	20	http://purl.obolibrary.org/obo/HAO_0000537
fu2	mesofurca	The furca that is not paired, arises from the mesopectus and continuous with the mesodiscriminal lamella.	19, 23A–F	http://purl.obolibrary.org/obo/HAO_0000547
	mesofurcal bridge	The apodeme that connects the lateral mesofurcal arms and corresponds to the site of origin of the dorsal mesofurco-profurcal muscle.	23D	http://purl.obolibrary.org/obo/HAO_0000548
	mesofurcal invagination	The invagination that forms the mesofurca.	23A–F	http://purl.obolibrary.org/obo/HAO_0002561
fup2	mesofurcal pit	The furcal pit that is located in the mesothorax.	13–14	http://purl.obolibrary.org/obo/HAO_0000549
	mesopectus	The sclerite that is U-shaped in cross section, connected anteriorly with the pronotum and the propectus, dorsally with the basalare, the mesonotum, the second axillary sclerite and the subalare, posteriorly with the metapectus and bears the mesodiscriminal lamella and the mesofurca.		http://purl.obolibrary.org/obo/HAO_0000557
	metapectus	The area that is located anteriorly of the metapleural carina.		http://purl.obolibrary.org/obo/HAO_0001270
	netrion	The area that is located posteroventrally on the pronotum and corresponds to the site of origin of the first flexor of the fore wing muscle.		http://purl.obolibrary.org/obo/HAO_0000644
pacp	postacetabular pits	Paired submedian pits located just posterior to the acetabular carina.	1, 3, 14	http://purl.obolibrary.org/obo/HAO_0002562
vbp	ventral bridge of pronotum	The area that connects ventrally the left and right halves of the pronotum.	4	http://purl.obolibrary.org/obo/HAO_0001055
	posterior mesepimeral area	The area that extends along the posterior margin of the mesopleuron and is delimited anteriorly by the mesepimeral sulcus.		http://purl.obolibrary.org/obo/HAO_0000751

Table 3. Mesosomal characters in platygastroid families. **1.** netrion: 0 absent, 1 present; **2.** pl2-3ax2 origin: 0 from mesopectus, 1 from mesopectus and from pronotum; **3.** ventral bridge of pronotum dorsal extension: 0 not extending dorsally, 1:extending dorsally; **4.** mesodiscrimen: 0 absent, 1 present **5.** mesodiscrimen structure: 0 only posteriorly, 1 present and extending anteriorly to the acetabular carina; **6.** mesodiscriminal lamella anterior end: 0 adjacent anteriorly with the acetabulum, 1 not adjacent anteriorly with the acetabulum; **7.** anterior mesofurcal pit: 0 absent, 1 present; **8.** anterior mesofurcal pit position: 0 near the middle of the ventral mesopectus, 1 anterior 1/3rd of the ventral mesopectus; **9.** setose median pit on acetabulum: 0 absent, 1 present; **10.** median invagination of acetabulum: acetabular carina medially enclose a pit-like structure without any distinct invagination: 0 absent, 1 present; **11.** mesofurcal bridge: 0 absent, 1:present; **12.** postacetabular pits: 0 absent, 1 present, **13.** mesepimeral sulcus and the posterior mesepimeral area: 0 absent, 1 present; **14.** mesepimeral ridge position: 0 extends along the posterior margin of the mesopectus, 1 extends anterior to the posterior margin of the mesopectus; **15.** pl2-3ax3 origin: 0 exclusively from the metapectus, 1 partially from the mesopectus. ? = not observed, na = not applicable.

Family/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Geoscelionidae	?	?	0	?	?	?	0	na	0	0	?	0	1	?	?
Janzenellidae	0	0	0	1	0	1	0	na	0	0	0	0	1	1	1
Neuroscelionidae	0	?	0	1	1	0	0	na	0	0	1	0	1	1	?
Nixoniidae	1	1	1	1	1	0	0	na	1	0	1	0	1	1	1
Platygastridae	0	0	0/1	0	na	0/1	0/1	0/1	0	0	0	0/1	0	0	0
Proterosceliopsidae†	0	?	0/1	1	?	?	0	na	0	0	?	0	1	?	?
Scelionidae	1	1	0/1	1	1	0	0	na	0	0/1	1	0	1	1	1
Sparasionidae	1	1	1	1	1	0	0	na	0	0/1	1	0	1	1	1



Figures 1–4. Mesopectus, ventrolateral view **1** *Amitus* ([USNMENT00989622_2](#)) **2** *Fidiobia* ([OSUC 698059](#)) **3** *Iphitrachelus* ([USNMENT01029164](#)) **4** *Sceliotrachelinae* sp. ([OSUC 698061](#)).



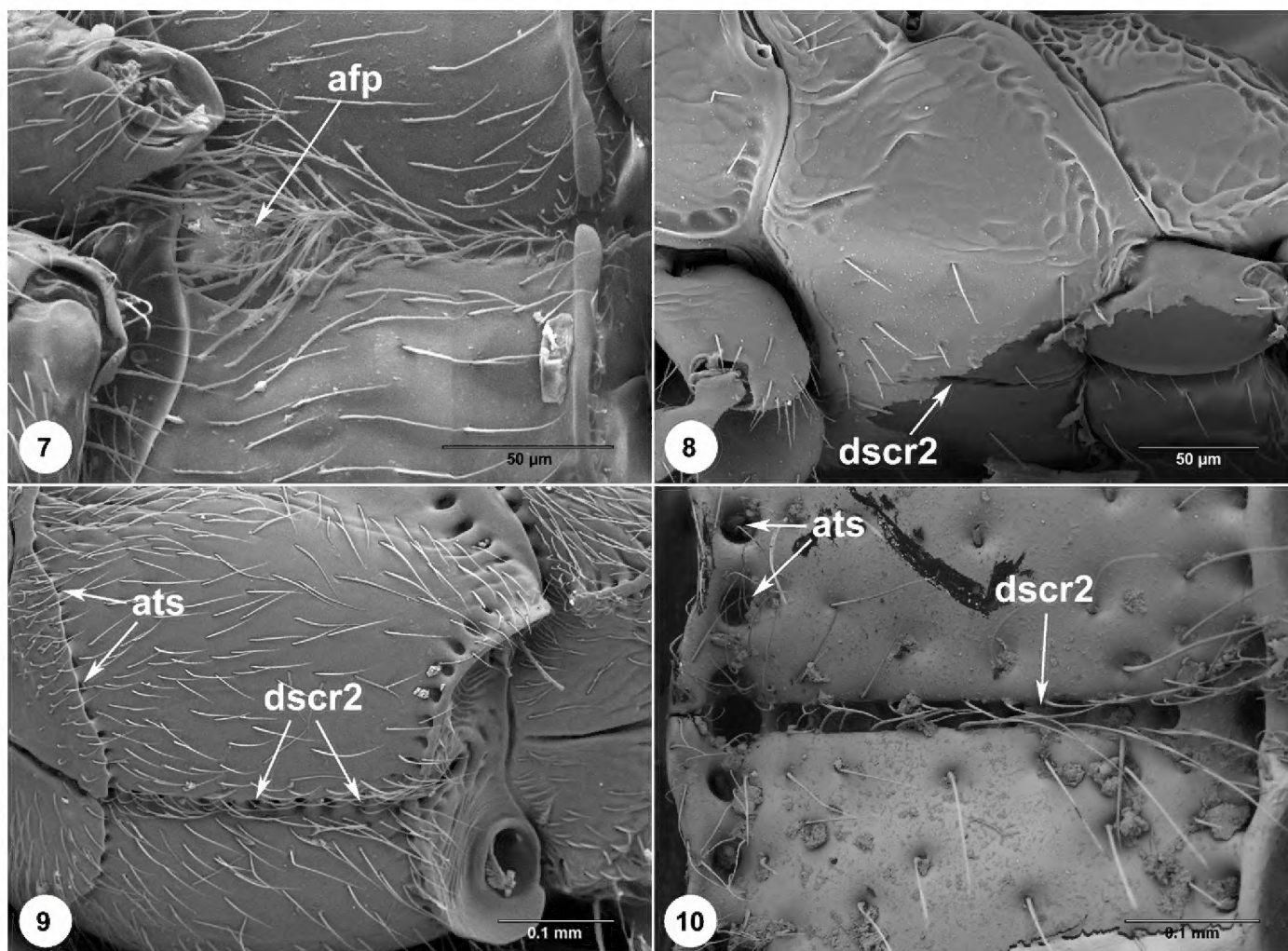
Figures 5–6. Mesodiscrimenal lamella **5** *Synopeas* sp. (UNHC_1046722B) **6** *Amitus* sp. (UNHC_1046725B).

The mesodiscrimen is absent from Platygastridae (4:0; Figs 1–4), present only posteriorly in Janzenellidae (5:0; Fig. 8), and present and extending anteriorly to the acetabular carina in other platygastroid families (5:1; Figs 9–12). The mesodiscrimenal lamella is not adjacent anteriorly to the acetabulum (6:1) in Janzenellidae and Platygastridae (except *Synopeas*), and in the latter, its anterior-most point is marked by the anterior mesofurcal invagination (Figs 6, 15, 17). The lamella extends anteriorly to the acetabulum (6:2; Fig. 5) in *Synopeas* (Platygastridae) and the other taxa examined.

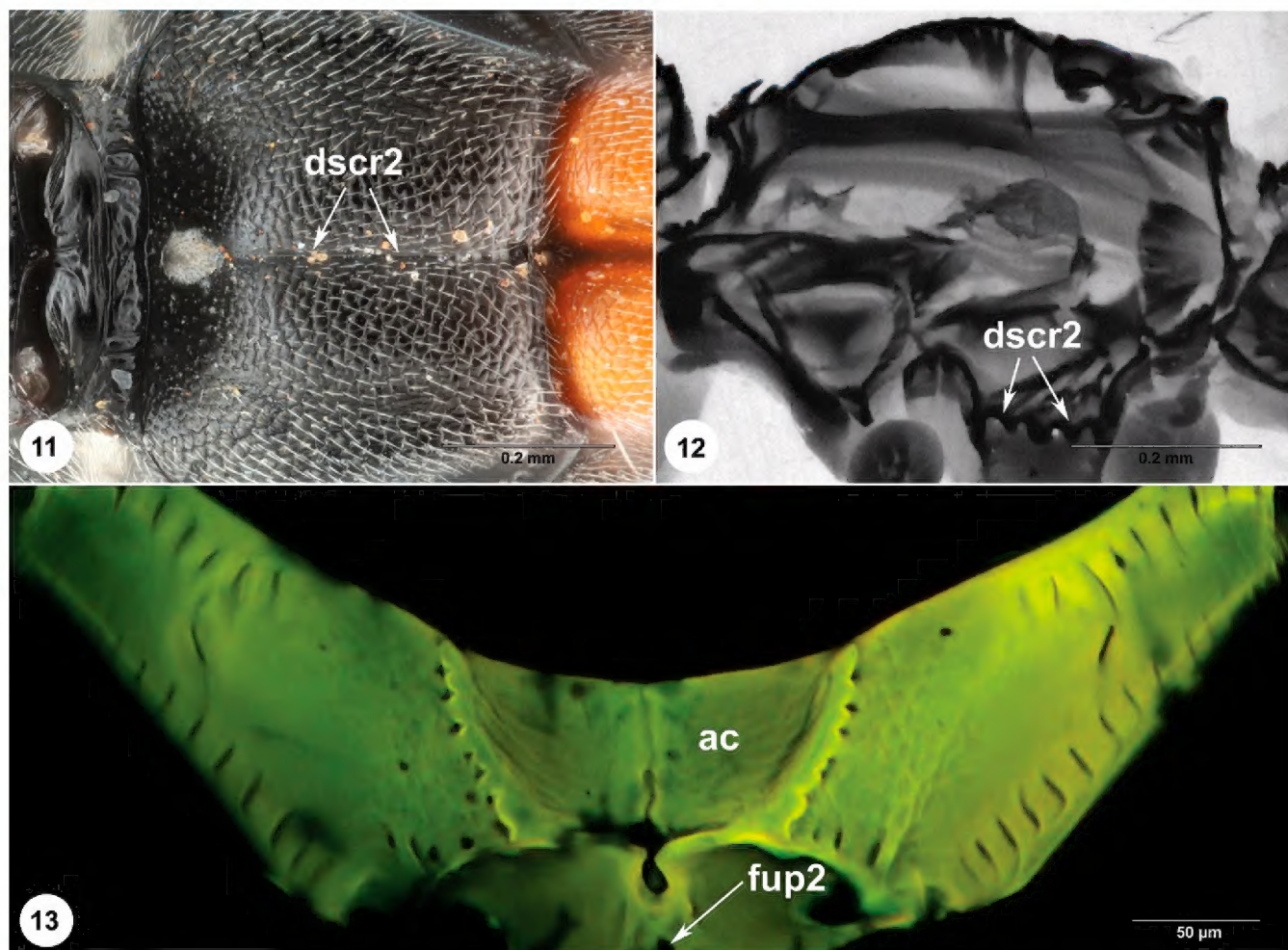
The anterior mesofurcal pit is present (7:1; Figs 1–4, 6–7, 14–17) in all Platygastridae except *Synopeas* and is absent (7:0; Figs 8–13) from other platygastroid families. The pit marks the anterior mesofurcal invagination that is continuous with the invagination of the mesofurca (Figs 15, 17). The anterior mesofurcal pit is located more posteriorly, near the middle of the ventral mesopectus (8:0; Fig. 3), in *Sacespalus*, *Iphitrachelus*, and *Inostemma*, and the pit is in the anterior third of the ventral mesopectus in other Platygastridae (8:1; Figs 1, 2, 4).

In Nixonidae, a setose pit is present on the acetabulum that does not correspond to an invagination and is not connected to the mesofurcal invagination (9:1; Fig. 11). The pit is absent from the other taxa examined (9:0). In *Gryon aetherium* (Scelionidae), the left and right halves of the acetabular carina medially enclose a pit-like structure without any distinct invagination (10:1; Fig. 13). The medial invagination is absent from other platygastroid families (10:0).

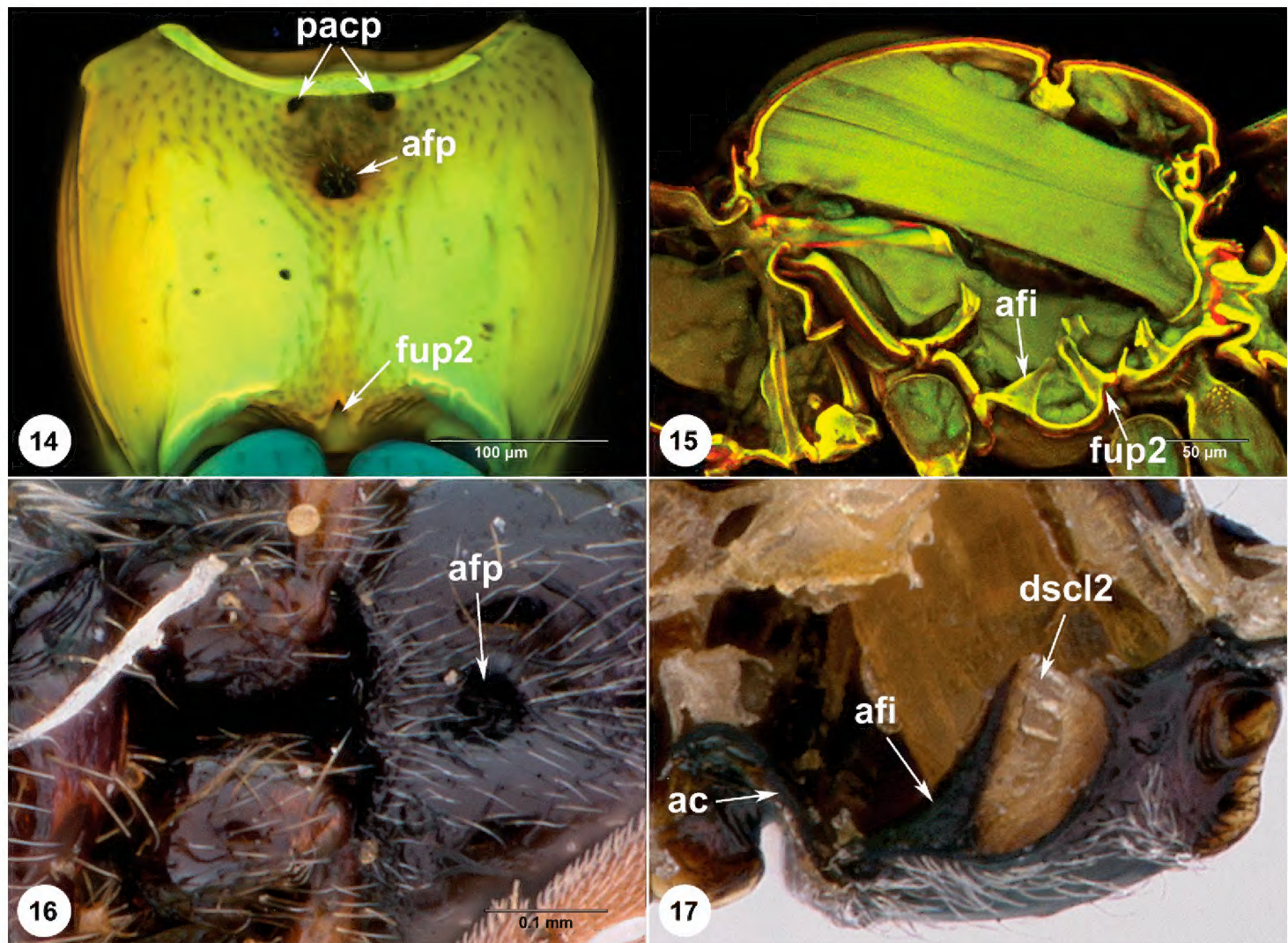
The mesofurcal bridge is absent (11:0; Figs 18–21, 23E, F) from Platygastridae and Janzenellidae and is present (11:1; Fig. 23D) in other platygastroid families.



Figures 7–10. Mesopectus, ventral view **7** *Orwellium enigmaticum* (OSUC 226542) **8** *Janzenella innupta* (OSUC 264384) **9** *Archaeoteleia gracilis* (OSUC 163002) **10** *Sceliomorpha* (USNMENT00989930).



Figures 11–13. **11** *Nixonia* (SAM-HYM-P093322), mesopectus, ventral view **12** *Proteroscelio* (CNU-HYM-MA-2017545), internal mesosoma, lateral view **13** *Gryon aetherium* (DPI_FSCA 00008713), mesopectus, ventral view.



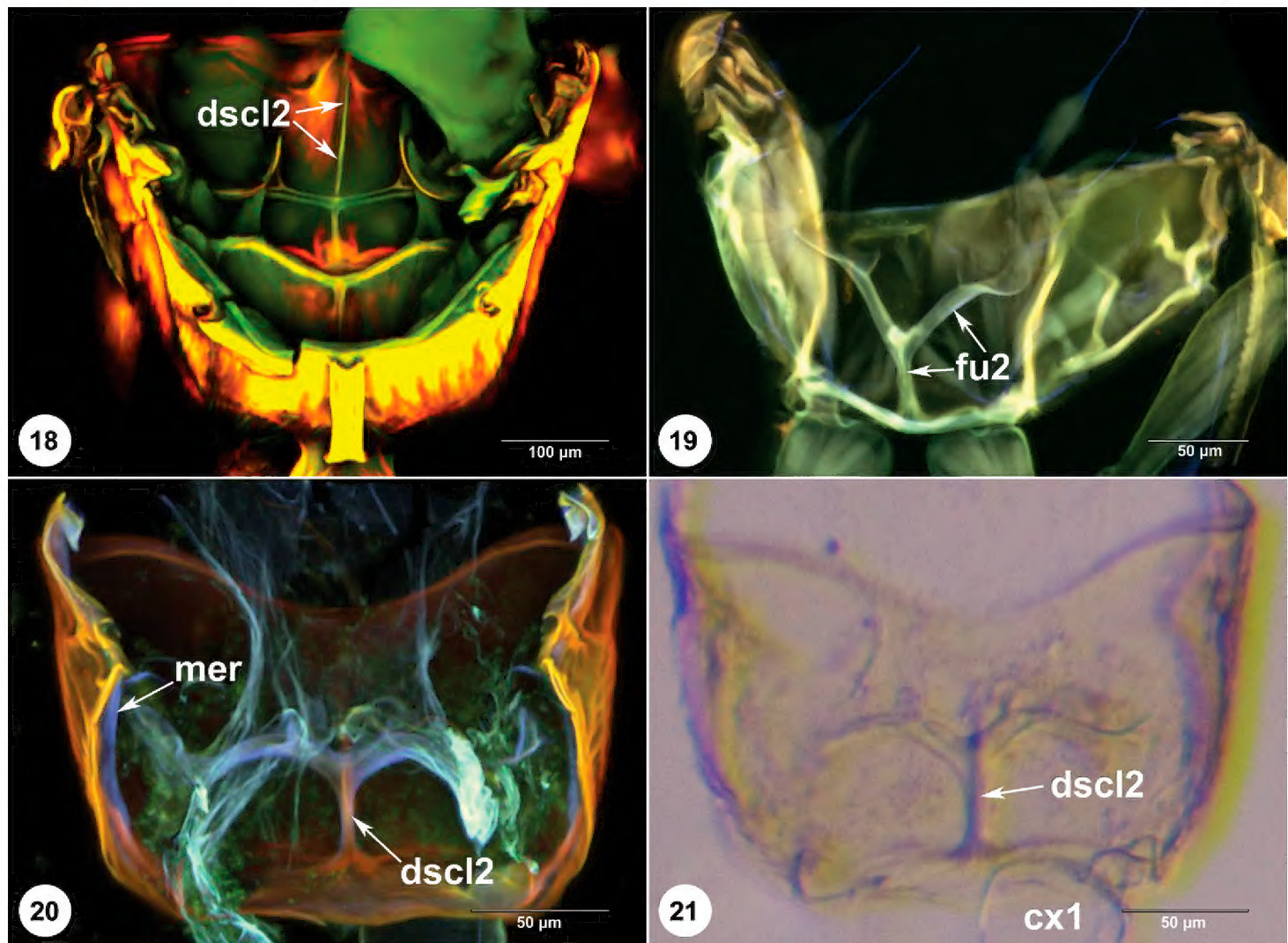
Figures 14–17. **14** *Trichacis* sp. (FSCA 00000276), ventral view **15** *Amitus* (UNHC_1046725A) interior of head and mesosoma, lateral view **16** *Isocybus* (OSUC 334137), mesopectus, ventral view **17** *Isocybus* (unvouchered), interior of mesopectus, lateral view.

Paired, shallow postacetabular pits are present (12:1; Figs 1, 3, 14) in many platygastroid genera (e.g. *Amitus*, *Alfredella*, *Oligomerella*, *Fidiobia*) and absent from other platygastroid families (12:0; Figs 2, 4).

In Platygastriidae, the mesepimeral sulcus and the posterior mesepimeral area are absent (13:0; Figs 1–4), the mesepimeral ridge extends along the posterior margin of the mesopectus (14:0; Figs 19, 20), and the first flexor of the hind wing arises exclusively from the metapectus (15:0; Fig. 23C). In other platygastroid families, the mesepimeral sulcus and posterior mesepimeral area are present (13:1; Fig. 9) and the mesepimeral ridge is anterior and parallel to the posterior margin of the mesopectus (14:1). The first flexor of the hind wing arises partially from the mesopectus in Janzenellidae, Nixoniidae, Scelionidae, and Sparasionidae (15:1; Fig. 23A, B). The muscle was not observed in other families.

Discussion

The external mesopleuron and metapleuron of Platygastriidae are simpler than most other platygastroid families (Masner 1979, 1980; Masner and Huggert 1989), however, this simplicity belies an array of internal characters that are demonstrably informative.



Figures 18–21. **18** *Synopeas* sp. (UNHC_1046722A), interior of mesosoma, dorsal view **19** *Allostema* sp. (FSCA 00000289), internal mesopectus posterior view **20** *Janzenella innupta* (UNHC_0032469), interior of mesosoma, dorsal view (CLSM) **21** *Janzenella innupta* (UNHC_0032469), interior of mesosoma, dorsal view (compound microscopy).

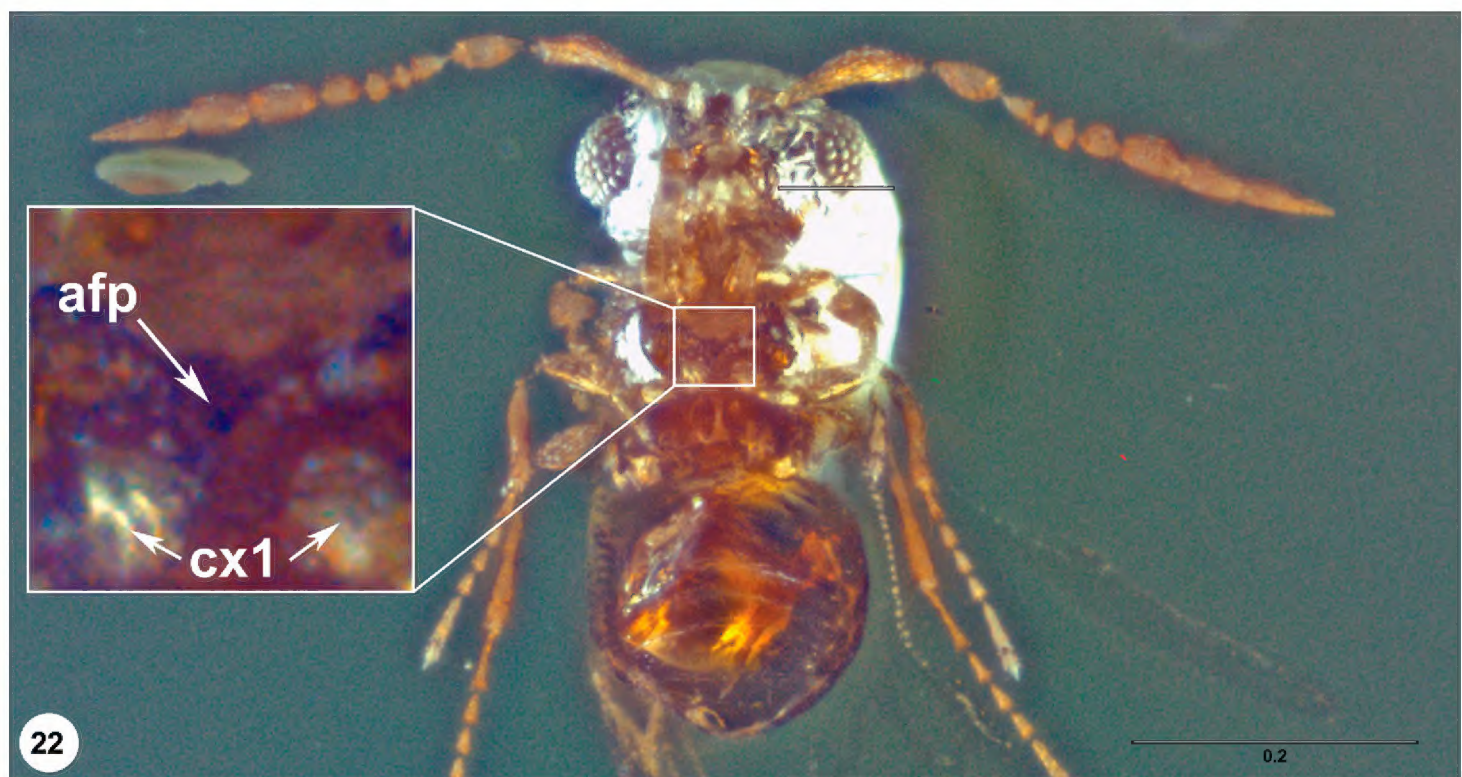


Figure 22. Platygastriidae in Burmese amber (CNU-HYM-MA-2016107), habitus, ventral view.

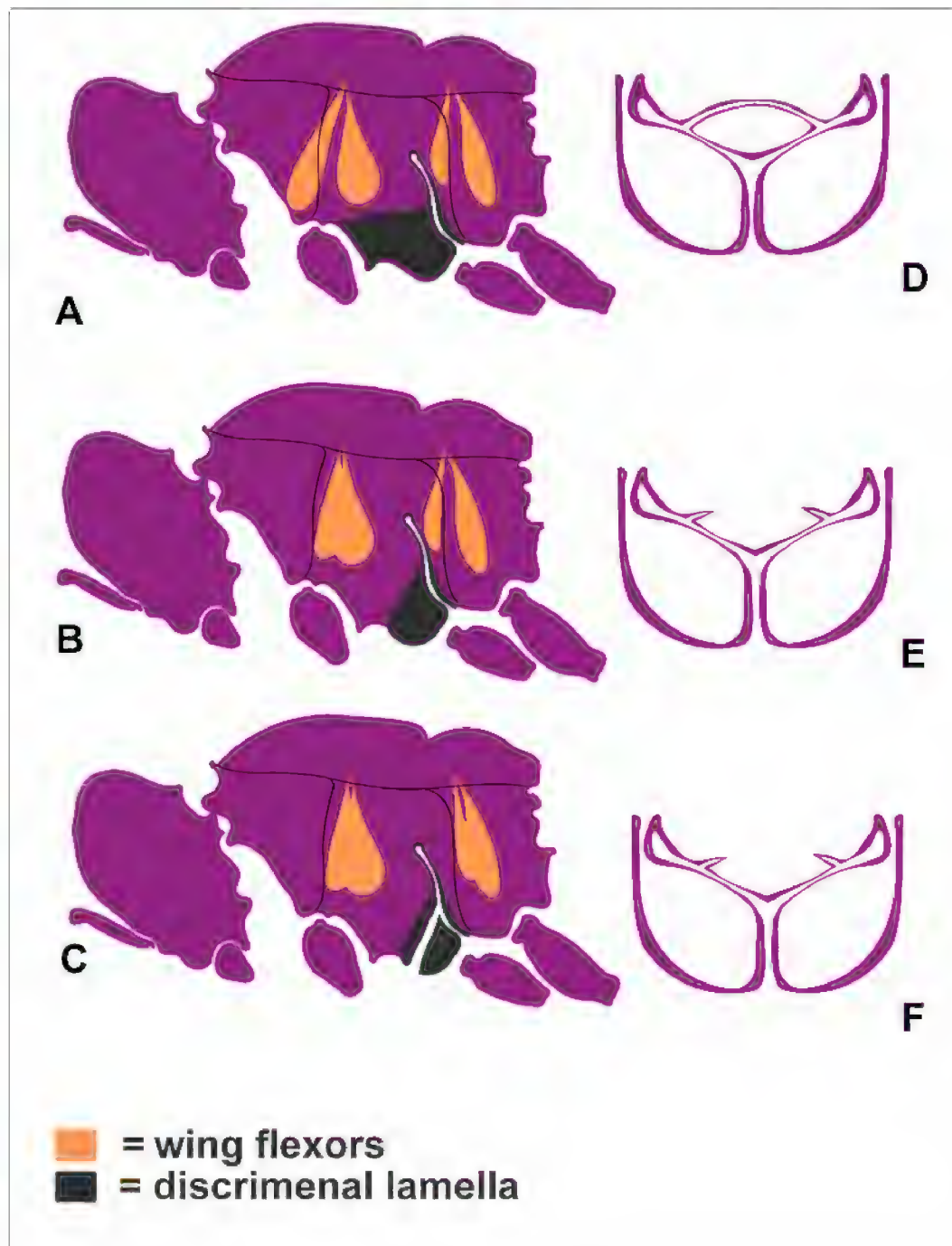


Figure 23. Illustration of the mesodiscrimenal lamella, invaginations on the ventral mesopectus, sites of origin of first wing flexors (**A–C**), and configuration of the mesofurca (**D–F**) **A, D** Scelionidae, Nixoniidae, Sparasionidae **B, E** Janzenellidae **C, F** Platygastriidae.

Our observations on pectal morphology provide a clear example of this. The proposed synapomorphies have utility for family-level identification and phylogenetic inquiry, which is especially useful for fossil taxa that often exhibit forms quite different from the extant fauna. For example, the anterior mesofurcal pit is recognizable in a specimen from Burmese amber, which contains the oldest representatives of Platygastriidae (Fig. 22). This specimen is recognizable as a platygastriid by other characters, but only the ventral aspect is presently visible. This confirms the association of the anterior profurcal pit with Cretaceous Platygastriidae and illustrates how this character may be helpful for family-level placement of fossil specimens. Similarly, in a bisected specimen of *Proteroscelio* Brues, a mesodiscrimen that extends anteriorly to the acetabulum is clearly indicated by a row of foveae (Fig. 12), as in *Nixonia* and *Archaeoteleia*. The

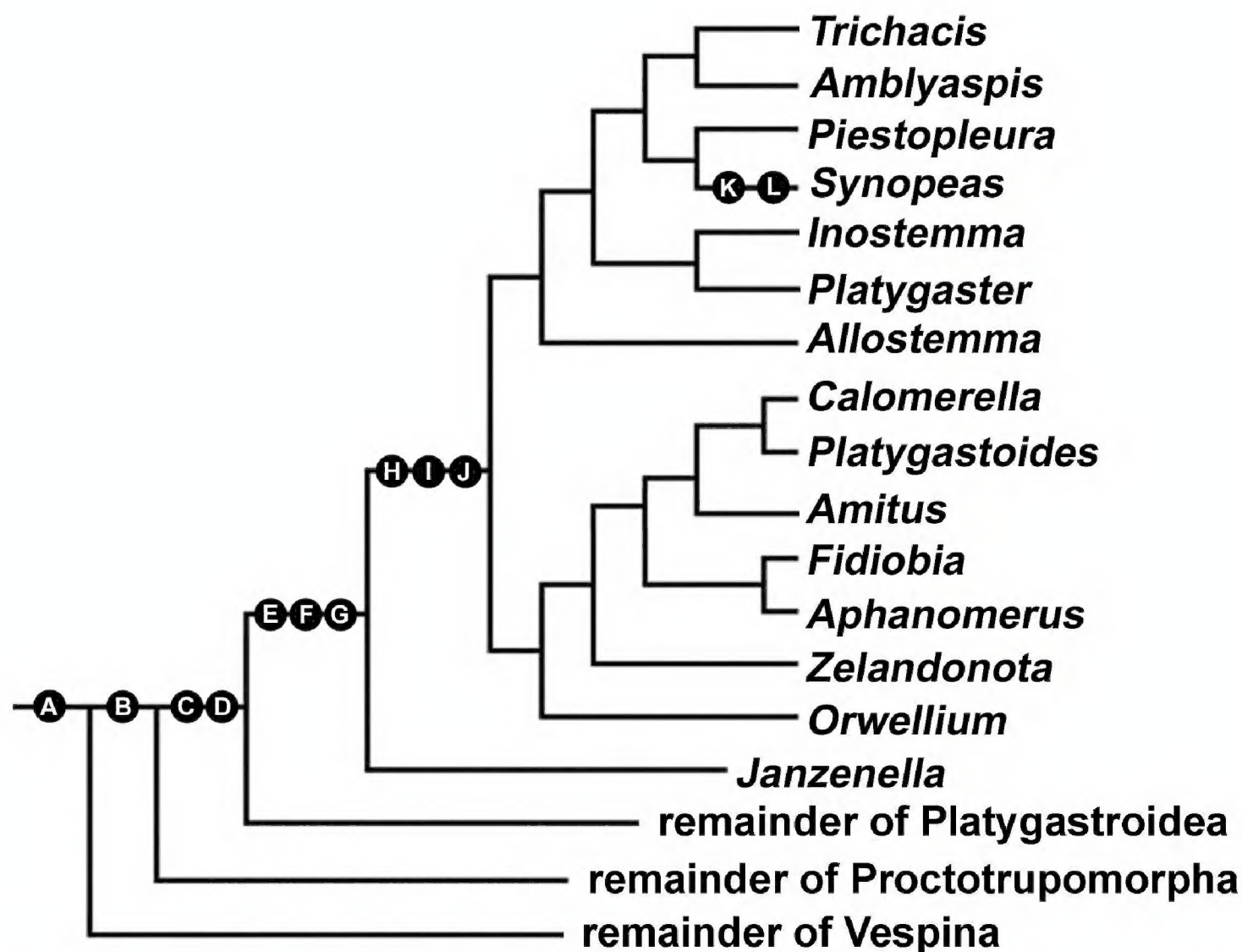


Figure 24. Modified phylogeny from Chen et al. (2021) with characters mapped to the topology. Parenthetical numerals indicate the corresponding character: state from Table 3 **A** mesofurcal bridge present (13:3) **B** mesepimeral sulcus present (13:1) **C** first flexor of the fore wing with pronotal site of origin (2:1) **D** first flexor of the hind wing with mesopectal site of origin (15:1) **E** discrimenal lamella not extending anteriorly to acetabulum (6:1) **F** mesofurcal bridge absent (11:0) **G** first flexor of the fore wing with mesopectal site of origin (2:0) **H** mesepimeral sulcus absent (13:0) **I** first flexor of the hind wing with metapectal site of origin (15:0) **J** anterior mesofurcal pit present (7:1) **K** discrimenal lamella extending to acetabulum (6:0) **L** anterior mesofurcal pit absent (7:0).

family-level placement of *Proteroscelio* is equivocal and may be guided by further examination of its mesosomal morphology.

Janzenella was described by Masner and Johnson (2007) with an uncertain position in the superfamily. The genus was later retrieved as sister to Platygastriidae in the phylogenetic analysis of Chen et al. (2021). We found that *Janzenella* is a morphological “missing link” because characters are shared exclusively with Platygastriidae while some plesiomorphies associated with the rest of the superfamily are retained (Table 2). The recent study by Bremer et al. (2021) documented characteristics of the pro-, meso- and metafurca in a specimen of *Janzenella* from Baltic amber, confirming the stability of these characters in Janzenellidae and demonstrating how emerging technologies can be applied to fossil taxa. In the case of Platygastroidea, this line of inquiry is clearly fruitful, as some of the most informative family-level characters are internal skeletomusculature.

We suspect that the anterior mesofurcal pit and its corresponding invagination, loss of the mesofurcal bridge, and ancestral wing flexor muscle patterns are inter-related, and that stabilization of the mesofurca shifted to mesofurcal invaginations from the mesofurcal bridge in concert with repositioning of wing flexor muscles. This makes sense considering that the mesofurca serves as the site of origin of numerous muscles involved in flight (e.g. mesofurco-mesolaterophragmal muscle) (Vilhelmsen et al. 2010). We also surmise that the transepisternal line is related to these characters. In Platygastriidae, the transepisternal line externally marks the ventral margin of the site of origins of the fore wing flexors (pl2-3ax2a, b) and the retractor of the mesoscutellum (pl2-t2b; Mikó et al. 2007), similar to some Cynipoidea and Diapriidae (Vilhelmsen et al. 2010). Thus, the presence of the transepisternal line might indicate a shift of the first flexor to the mesopectus, given that the line is absent from platygastroids where the first flexor arises from the pronotum (Mikó et al. 2007). The fossil genus *Proterosceliopsis* Ortega-Blanco, McKellar & Engel (Proterosceliopsidae) offers some additional clues. It has a mesepimeral sulcus, suggesting that the first flexor of the hind wing attaches on the mesopectus. The laterally visible ventral bridge of the pronotum in *Proterosceliopsis*, termed the netrion in Talamas et al. (2019), is similar to the condition found in Platygastriidae (Talamas et al. 2021), leading us to believe that the first flexor of the fore wing arises from the mesopectus in this genus. If this is correct, *Proterosceliopsis* would have the same configuration of first wing flexor muscles as *Janzenella*. Platygastriidae and *Proterosceliopsis* are the only platygastroids with a transepisternal line, which further supports the notion that there are mesopectal origins of first flexors of the fore wing in the latter taxon.

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